SOME ASPECTS OF THE POPULATION DYNAMICS OF THE BAT, *RHINOPOMA HARDWICKEI* IN A CAVE SYSTEM[1]

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(*With three text-figures*)

Data on some aspects of the population dynamics of *Rhinopoma hardwickei* were obtained between August 1978 through December 1980 are given. Banding recoveries and multiple recaptures indicate that *R. hardwickei* do not migrate, showing high degree of philopatry throughout the study period. The sex-ratio was about 0.6:0.4, although different behaviour of the sexes may lead to biased sampling techniques. More males than females of the species studied were captured, but this is not interpreted to indicate a differential mortality. That would mean that both sexes exhibit similar survival rate. Since social behaviour in bats does not seem to limit population size (Twente 1955) that predation on bats by hawks, owls, owlets, falcon, shrews, snakes and other animals and possibly death from pesticide effects also may be the primary factors controlling population density. Population showed a slow increase during the study period. Natality and mortality curves nearly approximate exponential functions. The natality rate has been higher than the mortality rate throughout the study period. Probability of survival of females over the years after banding was constant and this resulted in constant fertility rate.

Introduction

In any population of living organisms, whether it is growing, declining or stable, there is a continual turnover of individuals through the process of birth, death, immigration and emigration. This process depends on the organisms' interactions with the environment and is affected by factors such as food availability, predation pressure and the competition between the individuals in a group for different resources. The schedule of survival and fertility constitutes the life history of an organism. The dynamics of a population, namely the changes in numbers and composition of a population, is a consequence of the life-history of the various individuals in a population. Such a study termed 'population dynamics' is essential in understanding the biology of bats.

The small insectivorous bat, *Myotis lucifugus* has been shown to have a rather remarkable life span of 24 years (Griffin and Hitchcock 1965). However such longevity records concern only exceptional individuals and such records are of little value in understanding the population dynamics of a species. Several studies have been made on the theoretical age structures for bat population (Twente 1955, Davis 1966) survival rate of young *M. austroriparius* (Foster *et al.* 1978), population ecology of the bat, *M. grisescens* (Tuttle 1975) and mortality of the bat, *Eptesicus fuscus*

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(Kunz 1974). These studies involve banding of bats are mainly concerned with the homing abilities and migratory patterns. Pearson *et al.* (1952) attempted to study the reproductive biology of *Corynorhinus rafinesqui* in nature employing wing banding.

Apart from Sarkar *et al.* (1980) there are no systematic field studies on population strategies reported for bats of South India. It is very difficult to estimate population parameters of nocturnal animals such as bats within a short span of time. The aim of this study is to evaluate some of the results obtained from single marking and multiple recapture methods.

Materials and Methods

The study cave lies very close to the pass of Nagamalai ridge, 8 km from the Madurai Kamaraj University campus (9°58′N, 78°10′E). The pass is called 'Kanavai Katha Bootham' (abbreviated KKB). The cave is occupied exclusively by a resident population of *R. hardwickei.* The following criteria were taken into consideration while selecting the banding site KKB: (a) easy accessibility to day time retreats and (b) possibility of easy visual observation of the roosting site. The presence of alternative roosting sites within a short radius also enabled me to recapture bats when necessary. The climate of this area is that of typical tropical plains with long and dry summers and mild winters. Weekly trips were made to KKB for banding from August 1978 to December 1978.

The bats were captured with nets brought to the laboratory in mosquito net cages and thin aluminium bands with numbers engraved on them, weighing *c* 200 mg were used for banding as suggested by Bonaccorso *et al.* (1976). Since these bands were flanged as specified by Stebbings (1978) there was no injury. One hundred bats were marked with coloured celluloid bird rings (Hughes, England). Males were marked on the right fore-arm and females on the left fore-arm. Wing membranes were not slit. Chewing of bands and irritation to wing membranes were not observed markedly in any of the study animals. Helpless young were not banded. The marked animals were taken back to the cave on the same night and released for free mixing. 646 males and 354 females of *R. hardwickei* were marked and released for the study of population ecology.

A total of one thousand bats were banded during a period of five months. The banded bats were recognizable from a distance of five metres at their day-time retreats with a small number of non-banded bats. The existence of banded bats could be clearly made out, even without seeing them, since the bands made a rustling noise, when the bats moved. Bands could be recognized even after a lapse of 24 months and the numbers were not disfigured. The bands did not seem to interfere with the normal activities of the bats.

Recapture

The bats were recaptured upon emerging from the cave mouth, on the first week of every month during the study period. About one hundred were recaptured in any given month. The sexes, reproductive condition and band numbers were noted. The bats were then released immediately. Recapture study lasted for twenty four months from January 1979 through December 1980.

Total Counts

Weekly visits were made to the cave at the time of emergence. The observer lay down on the rock facing the horizon to count the number of bats emerging for foraging. This caused no panic in their normal routine. Since the emerging bats and the twilight produce a complementary effect making the animal distinct, visual counts were possible. The bats were counted visually from August 1978 through December 1980.

Birth and Death Rates

Birth and death rates are dependent of age of individuals and of the size of the population. Migration will also cause marked fluctuation in population status. From the observed data, the estimation of existing banded animals and the size of the population can be drawn. Since life span and age structures of bats are not known, a crude method can be developed to compute the birth and the death rates of *R. hardwickei*. We can take advantage of the fact that the number of banded bats will change only through death and emigration, while the total number of bats will also be affected by birth immigration. The estimates of these two parameters were made in the following fashion.

Mortality Rate (μ_t)

μ = Mortality rate
Ti = Visual count in the month i
Ci = Total number captured in the month i
Ri = Recaptured banded bats in the month i

Estimate of the total number of bats at time i $\left.\right\} = \dfrac{Ri}{Ci} \times Ti$

Then,

$$\mu i,\ i\text{-}1 = \frac{\left[\dfrac{Ri\ 0}{Ci} \times Ti\right] - \left[\dfrac{Ri-1}{Ci-1} \times Ti - 1\right]}{1/2\left[\dfrac{Ri-1}{Ci-1} \times Ti - 1\right] + \left[\dfrac{Ri}{Ci} \times Ti\right]}$$

In words, this is the difference in the number of banded bats in the time intervals i – 1 and i. To calculate the rate per individual, the difference obtained is divided by the mean population estimate of banded bats during this period. Birth and immigration will not affect the number of banded bats, since these will not be banded.

Birth rate (λ)

The recruitment rate, which includes birth and immigrations, of a population can be calculated relating its mortality rate. The method employed was as follows:

Let

λ = Recruitment rate
μ = Mortality rate
Ti = Total counts in the month i

Then

$$i,\ i\text{-}1 = \left[\frac{Ti - Ti - 1}{Ti}\right] + (\mu i,\ i\text{-}1)$$

(or) Change in population/Individual-mortality rate (assumption underlying this is that the death and emigration rate are the same for the banded and total population).

Population of surveying over the year

Change occurs in the ratio of banded animals. This change does not occur at a relatively constant rate. So the rate of change over each month can be used to estimate the mortality over the year.

Therefore,

$(1 + \mu \text{ year}) = (1 + \mu i) \cdot (1 + \mu 2) \ldots (1 + \mu n)$

This is the probability of surviving through the specific year, for any individual, regardless of age and sex differences.

To have a comparative account of death and birth rates over a year, the following calculations were made:

Birth rate over a Yr. = $\lambda 1 + \lambda 2 + \lambda 3 \ldots \lambda 12$
Death rate over a Yr. = $\mu 1 + \mu 2 + \mu 3 \ldots \mu 12$

The relation between these two variables is therefore equivalent to the increase or decrease of *R. hardwickei* population in the study area.

Birth rates of sexes

The combined population of bats maintains themselves long enough. The outcome of recapture data unaffects the proportion of females in relation to males. Proportion of females remains quite constant around 29-35% of females in the population through the study period, hence, no evidence for differential mortality by sexes (Fig. 3). Then the birth rate of females alone can be drawn.

$$\text{Ideally the birth rate of females therefore} \left.\right\} \frac{\text{Birth rate}}{2}$$

Results

From the one thousand bats that were banded at the study cave, 1299 recoveries were made from January 1979 through December 1980. Of these 876 were banded males and 423 were banded females. Table 1 gives the details of recovered bats during the study period. The average number of recaptured banded bats was almost the same for any given month. The recoveries include multiple recapture (on different dates) of individual bats (Table 2). The total number of banded and unbanded bats handled during the study period is presented in Table 3. The sexes are treated separately.

The degree of recaptures in relation to the period after banding decreased after a lapse of time. Table 1 illustrates that the first month after banding, recaptures were relatively high. This gradually decreased as the duration between banding and recaptures increased. Multiple recaptures were very few but extend even upto seven times (Table 2). Frequency of recaptures for the second and the third times was more during the first few months. However, bats were recaptured even after two years. Efforts to locate the banded bats during this period at other alternate sites resulted in only one banded bat being recaptured in an adjacent cave at *Pannian Malai*. This suggests that *R. hardwickei* form relatively stable population showing great loyalty to their original roosting site.

Table 1 shows the population fluctuation of *R. hardwickei* during January through December 1980. The data was obtained by visual count while the bats emerged out for foraging. The word population is used here with a meaning to indicate the number of bats occupying the KKB cave. It is interesting to note that population has been steadily increasing throughout the study period.

Several features of population parameters of *R. hardwickei* are apparent from Table 4 and Figs. 1 and 2. It constitutes the birth rate, the mortality rate and the relation between birth and death rates. The relative proportion of recaptured banded females to that of recaptured banded males remained more or less constant throughout the study period (Fig. 3). This will indicate the equal survival percentage of sexes. Since proportion of females remained constant over the study period, the fertility rates were evaluated to be 0.0755 and 0.0695 in 1980 (Table 4 and Fig. 3).

The shape of the mortality curve (μ) has been similar to the birth rate curve (λ) over the study period (Fig. 1). However, lower mortality rate was observed as —0.226 against the higher birth rate which was as +0.290 during the study period. Probability of sur-

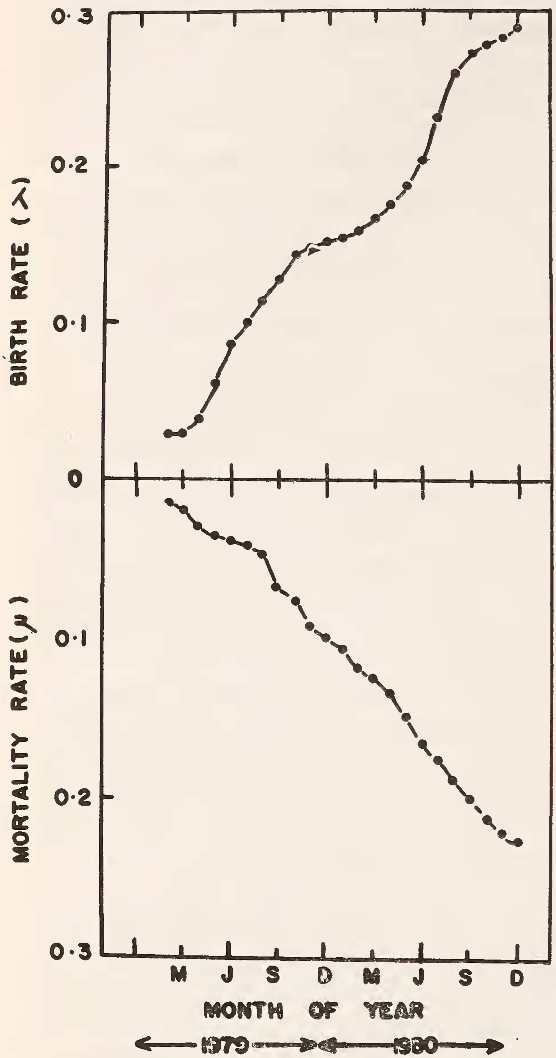

Fig. 1. Birth and death rates for *Rhinopoma hardwickei* population in the cave at KKB. Cumulative rates have been given for the years 1979 and 1980.

viving banded bats after two years showed an exponential decay (Fig. 2). Even so probability of surviving banded bats after two years is characterized by higher survival score of 0.796.

Discussion

This attempt of population analysis by banding is just a beginning for a full scale study of population dynamics. Though this should be continued for the entire life span of the species in question, the results from the present study are encouraging. Recapture rates and multiple recaptures were fairly high (Tables 1, 2 and 3) and banding produced no observable mortality. This is due to the continuous occupation of the same colony in the same cave and low migration rate, although there are a few alternative roosting sites available nearby. That means the colony is stable. The results show similarities to those of Pearson *et al.* (1952) in which the population of *Corynorhinus* was extremely stable. The frequency of recaptures both in relation to the number of times recaptured and the time lag indicate specificity for day time retreat as reported for some European congeneric species (Griffin 1970). These need not however, suggest that the territory of *R. hardwickei* is restricted, since it is possible that they might fly considerable distances for foraging, as several bird species are known to do (e.g. Ward and Zahavi 1973).

Population size was monitored with evening flight counts at the roost. Weather had a profound influence on bat behaviour and habitat use (Usman 1981). Numerous potential predators like owls, owlets, falcons, shrews and snakes frequented the roosts and its vicinity. Yet the fluctuation in the number of bats in the cave for any observed month was extremely limited which means that these bats normally do not migrate even for a short distance. Even during non-breeding season, the males and females were segregated in the same

TABLE 1

DETAILS OF RECAPTURES OF *R. hardwickei in* KKB

Month	Visual count	Recaptured banded males	Recaptured banded females	Captured unbanded males	Captured unbanded females	Total capture
1979						
J	934	48	24	18	8	98
F	976	47	23	21	10	101
M	981	46	22	22	9	99
A	1000	44	22	21	12	99
M	1030	44	21	26	10	101
J	1060	42	21	25	13	101
J	1078	43	20	26	14	103
A	1100	42	20	28	14	104
S	1138	40	21	30	17	108
O	1166	39	20	30	19	108
N	1190	39	19	31	21	110
D	1203	37	20	33	20	110
1980						
J	1215	38	19	35	20	112
F	1235	36	18	36	19	109
M	1251	35	16	36	18	105
A	1275	35	15	36	20	106
M	1310	32	15	37	20	104
J	1354	32	14	39	22	107
J	1407	29	14	43	19	105
A	1465	27	13	44	19	103
S	1503	27	13	44	23	107
O	1532	26	12	44	23	105
N	1553	24	11	42	22	99
D	1574	24	10	43	21	98

TABLE 2

RECOVERY ABSTRACT OF BANDED *R. hardwickei* IN KKB DURING 1979 AND 1980

Frequency	Recaptured banded males	% of recaptured banded males	Recaptured banded females	% of recaptured banded females	Recaptured banded bats (combined sexes)	% of recaptured banded bats (combinned sexes)
Once	173	26.78	225	63.56	398	39.80
Twice	142	21.98	30	8.48	172	17.20
Thrice	40	6.19	17	4.80	57	5.70
Four times	26	4.03	13	3.67	39	3.90
Five times	12	1.86	7	1.98	19	1.90
Six times	12	1.86	0	0	12	1.20
Seven times	9	1.39	0	0	9	0.90
Never recaptured	232	35.91	62	17.51	294	29.40

TABLE 3

TOTAL POPULATIONS AND SEX-RATIO OF *R. hardwickei* HANDLED AT KKB DURING THE STUDY PERIOD

Year	Banded males	Unbanded males	Banded females	Unbanded females	Total handled	% of males	% of females
1978	646	—	354	—	1000	64.60	35.40
1979	511	—	253	—	764	66.88	33.12
1979	—	311	—	167	478	65.06	34.94
1980	365	—	170	—	535	68.22	31.78
1980	—	479	—	246	725	66.07	33.93

roost but neither made any local migration, indicating a great fidelity to the roosting site as seen in for instance the gray bats (Tuttle 1976). Such a philopatry to a particular habitat appears to be a general phenomenon among bats (Humphrey and Cope 1976, Rice 1957). The exception to this is the roosting habit of a tropical microchiropteran bat, *Tadarida aegyptiaca* found close to my study area frequently. Large colonies of *Tadarida* have been noticed during my study to disappear overnight.

This spatial fidelity may result in overcrowding. Visual count exhibited a marked change in the population size during these years. It is obvious that there is also an upper limit to colony size beyond which increasing numbers are no longer advantageous. This limit may be determined primarily by the abundance of food resources available to the colony and by the availability of roosting sites (Tuttle 1976).

The birth and death rate curves (Fig. 1 and Table 4) from the observed data nearly approximate exponential functions. Caughley (1966) has shown that high juvenile morta-

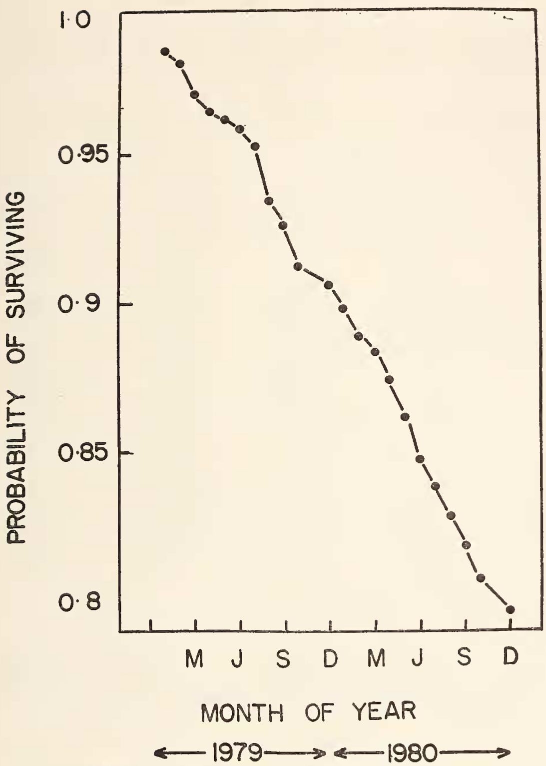

Fig. 2. Probable survivorship curve for *Rhinopoma hardwickei* population in the cave at KKB. Cumulative data are given for the years 1979 and 1980.

lity is an ubiquitous of mammalian survival patterns. Humphrey and Cope (1977) have emphasized that studies of bat survival beginning at or after weaning always misplace survival curves if study is short term. The same error occurs in all studies of animal survival in which the cohorts are marked sometime after birth (Foster *et al.* 1978). Ordinary population dynamics data are independent of age structure. If so a few legitimate interpretations are possible from the observed data for *R. hardwickei.* Figs. 2 and 1 show the annual change in survival potential. Loss during the second year after banding was greater than the first year. The mortality rate begins very low at —0.098 and claims to a higher annual rate at —0.128 in the second year. Birth in course of these years compensated the loss. We can envision this as a demographic adjustment necessitated by the higher mortality. Pearson *et al.* (1952) recognised a similar pattern of survival for lump nosed bats. The observed mortality includes the death of bats of all age structures. These are real rather than random deviations as observed by Davis (1966) for *Pipistrellus subflavus.* Davis (1966) pointed out that a change in the function will be apparent at the other end of the curve, as survival decreases beyond certain years and fall sharply as they approach maximum life span. Several species exhibit survival curves which approximate a constant percentage loss among all age groups (Davis 1966). This requires further study for confirmation. That would mean that an exponential decay curve would apply to an animal population if all losses are due to predation or decrease acting equally upon all age groups. Age is important in determining survival rates but its effects would be of gradual change. However, based on the frequency of bats captured by predators there was no apparent difference in the proportion of adults and juveniles preyed upon by these predators. Predation and the loss of babies falling to the floor account for most of the yearly mortality. Application of pesticides to the crops by the local farmers forms one of the causes to non-specific age related mortality.

Probability of surviving banded males and females, two years after banding showed high survival rates (Fig. 3) indicating high degree of tolerance. The survival percentage of females has been on par with the survival percentage of males throughout the study period (Table 4 and Fig. 3). Twente (1955) estimated that

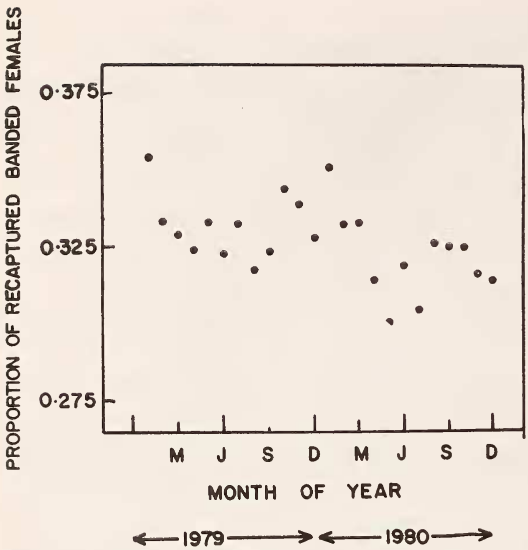

Fig. 3. Proportion of recaptured banded females of *Rhinopoma hardwickei* in relation to males over the study period.

in a population of bats in which each female has only one young per year, a constant of 66.7% survival rate (i.e. 33.7% = mortality rate) must operate if the population is to stay at the same size. *Rhinopoma* produces one young in a year. The birth peak occurs in May, June and July. Weaning extends upto November. The observed data on birth and death rates bear evidence for the continuous living of the colony in a particular cave and slow increase of population size.

TABLE 4

COMPARATIVE ACCOUNT OF BIRTH AND DEATH RATES OF *R. hardwickei* IN THE KKB CAVE OVER THE STUDY PERIOD

Month	1979		1980	
	λi	μi	λi	μi
J	—	—	0.002	—0.008
F	0.029	—0.014	0.005	—0.011
M	0.001	—0.004	0.007	—0.006
A	0.008	—0.011	0.009	—0.010
M	0.023	—0.006	0.012	—0.015
J	0.025	—0.003	0.016	—0.017
J	0.014	—0.003	0.028	—0.010
A	0.014	—0.006	0.028	—0.012
S	0.013	—0.020	0.013	—0.012
O	0.015	—0.009	0.006	—0.013
N	0.005	—0.015	0.005	—0.009
D	0.004	—0.007	0.008	—0.005
Birth and death rates over the years	0.151	—0.098	0.139	—0.128
Cumulative rates of birth and death over the study period			0.290	—0.226

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